A CENTURY AND A HALF OF PEPPERED MOTHS

L. M. Cook

The Manchester Museum, University of Manchester, Manchester M13 9PL.

IN PARTS OF Britain, the frequency of melanic forms of the Peppered Moth *Biston betularia* (L.) experienced a spectacular increase during the 19th century when melanic frequencies in other moths also increased. However, the species have responded in different ways to recent environmental changes, with the melanic form *carbonaria* Jordan of *B. betularia* undergoing a striking decline over the last two decades. Contributions to the entomological literature played a major part in demonstrating the patterns of change in both periods.

During the nineteenth century observations by various collectors were published independently (e.g. Stephenson, 1858; Edelston, 1864; Cooke, 1877; Chappell, 1886). Tutt (1891) noted the association of melanics with more humid regions and the possible advantage conferred by camouflage in the presence of visual predation. Bateson (1900) requested current and historical information from collectors in order that the pattern of change could be pieced together. The results were published by Barrett (1901) and by Doncaster (1906). These reveal increasing frequencies of melanics in towns and cities of the north of England from the middle to the end of the 19th century, by which time populations comprised over 90 per cent *carbonaria*. South of this industrial heartland, melanic forms increased in frequency at a later date, although they never rose in the rural West and Southwest. Steward (1977) mapped the dates of first records, which seem to show a migration into the more polluted regions south of the Severn-Wash line in the late 19th and early 20th century. The pattern of change was largely achieved by then.

Although the evidence showed some clear trends it was incomplete and patchy. There were very few quantitative records of early changes, partly because little attention was then paid to numbers. H.B.D. Kettlewell provided a quantitative picture by coordinating national surveys in the 1950s to the 1970s (Kettlewell, 1958, 1965, 1973). Kettlewell (1973) listed 175 recorders who contributed to his Appendix C, and these surveys revealed an essentially unchanging pattern.

Over the last two decades industrial environments have become cleaner and melanic frequency has declined. An invaluable record of the change was made by Sir Cyril and Lady Clarke at a site in north-west England (Clarke *et al.*, 1990, 1994; Grant *et al.*, 1996). This consists of yearly estimates of melanic frequencies based on large samples examined from 1959 to the present. Less complete series have been obtained for other parts of the country (Mani and Majerus, 1993; West, 1994; Grant *et al.*, 1998; Cook *et al.*, 1999). The increase and decrease in *carbonaria* frequency in the Manchester area over one and a half centuries is shown in Figure 1. Declines have also been observed in the Netherlands (Brakefield, 1990) and in the United States (in *B. b. cognataria*, Grant *et al.*, 1998). The recorded changes clearly demonstrate the selective process in action (Grant, 1999). Where figures from 25 years ago can be compared with those from the last few years, a striking pattern emerges. Cook (*in press*) analyses these changes in more detail. Figure 2 gives a

general indication of the trend. The points would lie along the diagonal line if there had been no change. The line through them has a slope of 0.257, indicating that on average frequencies are now only a quarter of what they were. Where *carbonaria* was already rare it has declined little, but where it was at high frequency the change has been as rapid and extreme as any that occurred during the nineteenth century. Industrial melanism in the Peppered Moth is coming to an end.

The Peppered Moth story is a celebrated example of a change in gene frequency under selection, that is, of the raw material of evolution. Two points cannot be stressed enough. First, our knowledge of the changes has, and will continue, to depend significantly on the work of those who record local occurrences. All information obtained is worth publishing, as individual records which apparently contribute nothing may illustrate patterns when combined with others. Second, the precise reasons for changes are not fully understood. The story has been recently discussed by Majerus (1998), who points out the gaps in our knowledge. Selective predation by birds is probably the most important cause of change, but just how selection relates to the moths' resting background (Mikkola, 1984; Howlett and Majerus, 1987) needs further investigation, as do factors unrelated to appearance, such as differential pre-adult survival (Creed *et al.*, 1980) which may also influence gene frequency.

In trying to unravel the causative agents we are hampered by the fact that even the ecology of the species is incompletely known. Models which predict the patterns reasonably well assume low population densities and high migration rates (Cook and Mani, 1980; Mani, 1990). More observations relating to numbers and movement would be of great value. In this context, it is worth reporting some data on trapping

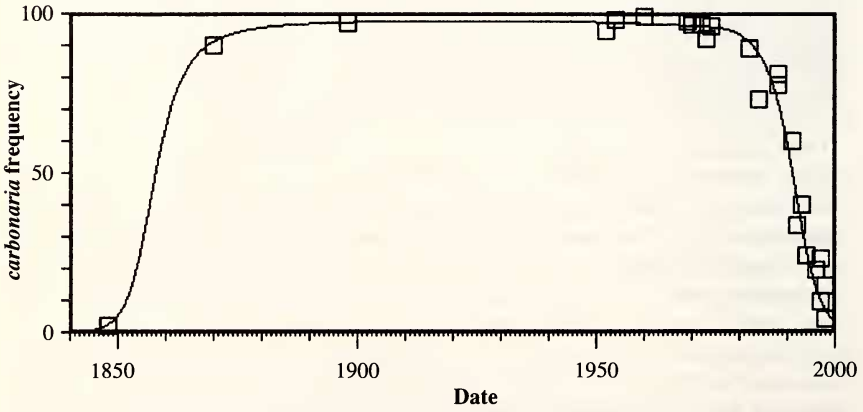

Figure 1. The apparent change in frequency of the *carbonaria* form of the peppered moth in the Manchester area. Data taken from a variety of sources summarised in Kettlewell (1973), Bishop *et al.* (1978) and Cook *et al.* (1999). The first three points are based on impressions by contemporary writers, the rest on samples of varying sizes.

success by students with no special interest in Lepidoptera. In a survey run by Dr M.E. Varley for the Open University, students were provided with mercury vapour light traps, asked to run them over one or two periods of five nights each and to record the numbers and types of Peppered Moths caught. These records were then returned with information on locality. From 1983 to 1987 one specimen of each of the forms collected was supplied for verification (Cook, Mani and Varley, 1986). The survey provided a random sample from a broad range of sites in the United Kingdom. Overall catch rate was quite low, never exceeding 0.4 moths per night. The maximum number collected in a 5-night period was 40 and the most common non-zero value was 1 (Table 1). There was significant heterogeneity between years ($P<0.001$), with particularly low densities in 1984 and 1987. As a rule females fly only if they fail to mate where they emerge. About 4 per cent of the voucher specimens were female, suggesting that such failure is quite common, which would be consistent with low average densities.

Table 1. Trapping success in Open University survey. Peppered moths caught in five-night periods of m.v. trapping at sights picked at random in the UK.

Year	1983	1984	1985	1986	1987
Total five-night trapping periods	984	1043	276	526	1033
Total moths caught	1292	521	475	1016	385
Mean catch per night	0.26	0.09	0.34	0.39	0.07
Per cent female in voucher sample	4.1	4.1	5.1	2.4	4.3

Students were also asked to state whether their collecting area was urban or rural. This classification is highly subjective since one person's town may look rural to another, but it does provide some indication of the nature of a site. In 1983 there were 502 rural and 482 urban sites. Of the sites with 6 or more insects, 45 (9.0 per cent) were rural and 13 (2.7 per cent) were urban. This difference is significant ($P<0.001$) suggesting that good catches are more likely to be made in the country than in town. Experienced observers such as the Clarkes may obtain hundreds of moths in a season (e.g. see Clarke *et al.*, 1990a, 1990b, 1994). Their daily records can now be consulted through the Manchester Museum. Over 35 years, their catch was more than 17,000 insects, less than 0.5 per cent of which were females (C. A. Clarke, personal communication). Traps are run for longer periods, however, sometimes with the added attraction of assembling females, and high densities probably indicate fortunate trapping locations. The general picture is of low densities, fluctuating from year to year with lower averages in urban areas and occasional localities of high abundance.

Almost all the work referred to above has benefited in some way from data provided by lepidopterists. This includes the early development of the pattern, the period of stability examined by Kettlewell and much of the evidence for decline. The evidence that different genotypes may have different survival rates (Creed *et al.*, 1980) comes from analysing published breeding results dating back as far as Greening (1863), before the birth of Mendelian genetics. Owen (1996) referred to the declining frequency and requested data on catches. The response allowed the change over the last 25 years in many parts of the country to be recorded (Grant *et al.*, 1998) and provides the majority of the points in Figure 2. The address for further data is given by Owen (1997). As the rise and fall of the melanic forms in the

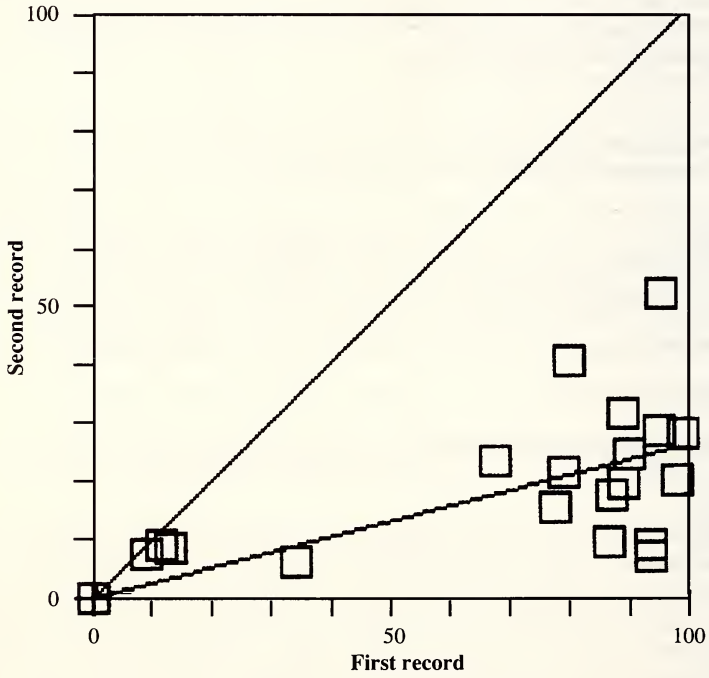

Figure 2. Frequency of *carbonaria* in *Biston betularia* about 25 years ago compared with recent frequencies for a range of British localities. Data from Mani and Majerus (1993), West (1994), Grant *et al.* (1998) and Cook *et al. 1999).*

peppered moth comes to its conclusion, records continue to be invaluable, either sent to a coordinator or published separately. Equally important are data from other species with melanic forms, which may or may not show parallel changes in frequency. The Scalloped Hazel *Odontoptera bidentata* Clerck and the Pale Brindled

Beauty *Phigalia pilosaria* ([D.& S.]) are of particular interest, because records exist of distribution of melanics at earlier periods. In both *P. pilosaria* (Lees, 1981) and *O. bidentata* (Cook and Jacobs, 1983 and personal observation) the response to changing conditions has been less marked than in the peppered moth. For all the species involved we still know too little about larval and adult ecology, adult resting positions, dispersal patterns and population density. Some years ago Majerus (1990) pleaded for data to be published. As he says in his book on melanism (Majerus, 1998), "There is, perhaps, no other field in which the amateur lepidopterist can contribute more usefully to scientific research with so little effort beyond that which they normally devote to their hobby".

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